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THE COLOR SENSE OF THE HONEY-BEE: CAN BEES DISTINGUISH COLORS?

JOHN H. LOVELL

CAN bees distinguish between differently colored floral leaves? If they can not, then, a polychromatic flora possesses no advantage over one in which the flowers are all of the same hue. In the Alpine flora, says Kerner, on the heights above the tree-line, there is actually no spring and no autumn, only a short summer following a long winter. All the flowers have, therefore, to blossom in a short time. "White and red, yellow and blue, brown and green, stand in varied combination on a hand's-breadth of space."¹ These color contrasts, it is believed, enable bees easily to remain constant to a single plant species so that pollination is effected to the mutual advantage of both insects and flowers. If the flowers were visited indiscriminately, regardless of their form, much pollen would be wasted and not a little time and effort would be lost. Genera adapted to bees, according to Müller, display a variety of colors, especially when they bloom simultaneously in the same locality, as *Aconitum lycoctonum* yellow, *A. napellus* blue; *Lamium album* white, *L. maculatum* red, *Galeobdolon luteum* yellow; *Salvia glutinosa* yellow, *S. pratensis* blue; *Pedicularis tuberosa* whitish yellow, *P. verticillata* purple.

If the different colors were evolved, as I believe, because of the power and necessity in bees of discriminating between them then it is not wonderful to find represented among bee flowers not only white, yellow, red, violet, blue, brown and even blackish (*Bartsia*) in the most varied degrees, but also to see several colors in the same flower combined in manifold ways. I mention only *Polygala Chamæbuxus*, *Viola tricolor*,

¹ Kerner, Anton, "Natural History of Plants," translated by F. W. Oliver, 2, pt. 1, 198. Also see Plate XII., "Alpine Flowers in the Tyrol," drawn from nature by E. Heyn.

Cerinth major, *Galeopsis versicolor*, *Astragalus depressus*, *alpinus* and many other Papilionaceæ.²

On the other hand, it is asserted by Plateau that all natural flowers might be as green as their leaves without their pollination by insects being compromised;³ while in the opinion of Bethe bees are mere reflex machines and have no senses, or ability to make experiences and modify by them their actions.⁴ If either of these extreme claims is admitted, it is evident that a variety of colors can be of no benefit to flowers. It seems desirable, therefore, to consider what experimental evidence is available to prove that bees can distinguish differences in color.

It was first shown by Lubbock (Lord Avebury) that honey-bees can distinguish between "artificial" colors, or slips of paper of different hues. An account of his experiments is given at considerable length in his well-known book on "Ants, Bees and Wasps"; but, as they were performed more than thirty years ago, I shall describe a number of experiments made myself, in some of which the conditions have been varied. I shall endeavor to show not only that bees can distinguish between the colors of papers, of flowers and of painted hives, but that they can learn *not to discriminate* between them, when this is for their advantage. Their behavior in detail will likewise be carefully recorded.

On a pleasant September morning I accustomed a yellow (Italian) bee to visit a strip of blue paper⁵ three inches long by one inch wide. To prevent the paper from blowing away or becoming soiled it was covered with a

² Müller, Hermann, "Alpenblumen," p. 500. Knuth, Paul, "Handbuch der Blütenbiologie," 1, 141, or "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, 1, 117.

³ Plateau, Félix, "Les insectes et la couleur des fleurs," *L'Année Psychologique*, 13, 79.

⁴ Buttel-Reepen, H. v., "Are Bees Reflex Machines?" translated by Mary H. Geisler, p. 3. Bethe, Albrecht, "Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben?" p. 86. Emil Strauss, Bonn, 1898.

⁵ The colored papers used were obtained from the Milton Bradley Co., Springfield, Mass., and were produced in pure spectrum colors by having the surface coated. Stained papers have the colors somewhat broken.

transparent glass slide of the same dimensions, upon the center of which a small quantity of honey was placed. These slides are used for mounting microscopic objects, and may be obtained of any dealer in optical instruments for a trifling sum.

After the bee had made a number of visits to the blue paper, a red slide of the same dimensions, and prepared as described above, was placed six inches to the right of it. An equal quantity of honey was also placed upon the center of this slide. When the bee returned from the hive it alighted on the blue slide, which still remained in its original position.

On the departure of the bee for the hive the slides were transposed, *i. e.*, the red put in the place of the blue and the blue where the red had been. When the bee returned, and no longer found the blue paper in its usual position, it flew back and forth, examining both slides, paused for a second or two on the red, then resumed its flight, but finally settled on the blue. A little later it flew up into the air, but soon returned to the blue; then it flew across to the red, where it remained for the rest of its visit. The change in the position of the blue, and the discovery of a differently colored slide also bearing honey, evidently disturbed the bee; and its frequent flights showed that it was endeavoring to orient itself to these new conditions. As will now appear it did not find it necessary to repeat this course of reconnoitering.

While the bee was away I transposed the slides for a second time, the distance apart being as before—six inches. The bee returned directly to the blue. Twice it left the blue for a few moments, but each time returned to it.

When the bee left for the hive, I again transposed the slides; the bee returned to the blue. The bee left for the hive, and I transposed the slides. It returned to the blue.

While the bee was away I transposed the slides for the fifth time. The bee returned to the blue. Then it left the

blue slide, flew across to the red, but at once returned to the blue.

The bee left for the hive and I transposed the slides. On its return it circled about as though in doubt and presently disappeared from view; but a little later it returned and settled on the blue. While taking up its load of honey it left the blue three times, but in each instance returned.

The bee left for the hive and I transposed the slides. It returned to the blue.

The bee left for the hive and I transposed the slides for the eighth time. On returning the bee hovered close to the red, and then went to the blue.

As soon as the bee returned to the hive, I transposed the slides for the ninth and last time. When the bee came back, it alighted after a little hesitation on the blue. It left once and flew across to the red, but soon returned to the blue. Left a second time but soon returned. Then it flew into the room, and on being released went back to the hive.

There can be no question that in this experiment the honey-bee was able to distinguish the blue color from the red. I repeated the experiment many times and varied it in many different ways, but the bee always showed its ability to distinguish between differently colored slips of paper. Only one bee should be employed, for if there are two or three they will conflict and to some extent produce confusion.

For the purpose of comparison the following experiment, in which a larger number of colored slides was employed, was performed on the morning of September 20, six days after the experiment just related. A black or German bee, instead of an Italian bee as before, was accustomed to visit a blue slide prepared as described above. After a number of visits had been made, the blue slide was moved to the right about seven inches, and a red slide put in its place. The bee returned to the blue.

As soon as the bee left for the hive, the slides were

transposed. The bee returned to the blue. The bee again left for the hive and I transposed the slides. It returned to the blue.

When the bee left for the hive, I transposed the slides for the fourth time. The bee returned to the red, which was now in the place occupied by the blue at the time of its previous visit.

The bee left for the hive, but no change was made in the position of the slides. On its return it again sought the blue, showing that the influence of this color was still dominant, though it now knew from memory as well as from its visual and olfactory senses that honey was to be found on the red.

A yellow slide was now placed upon the board about seven inches to the left of the blue. The order of the colors was yellow, blue, red, and their distance apart seven inches. The bee returned to the blue. When the bee left, I transposed the yellow and blue so that the order was blue, yellow, red. The bee returned to the blue. On the departure of the bee I again transposed blue and yellow. The bee returned to the blue.

When the bee left for the hive, a white slide was introduced and the distances between the slides reduced to four and one-half inches. The order of colors was yellow, white, blue, red. The bee on its return flew back and forth several times over the slides, and after hovering in the air for a few moments in hesitation alighted on the white.

The bee left for the hive, but no change was made in the order of the slides; it returned to the blue.

When the bee left, a black slide was substituted for the white one. The order of the slides was yellow, black, blue, red and the distances apart remained as before four and one-half inches. The bee returned to the yellow, but soon left it (perhaps disturbed by a fly) and returned to the blue. No change was made in the order of the slides, and the bee returned to the black. But on its next visit it again sought the blue.

I now transposed the red and blue, bringing blue to the

extreme right so that the order was yellow, black, red, blue. The bee returned to the blue. The red and blue were again transposed, the bee returned to the black, but soon left it for the blue. Black and blue were then transposed, the bee returned to the blue. I next transposed yellow and blue, bringing blue to the extreme left, the bee returned to the red. No change was made in the order of the slides, the bee returned to the yellow. The slides were again left unchanged, the bee touched on black, then on red, but finally alighted on blue. Red and blue were transposed so that the order of colors was red, yellow, black, blue. The bee returned to the black. No change was made in the slides, the bee returned to the blue.

During the first five visits, when there were only blue and red slides, the bee returned four time to the blue and but once to the red. This single exception is not without value, since it shows that the bee had the power of choice, and that its behavior was not mechanical, or that of a reflex machine. During the next three visits blue, red and yellow slides were employed and the bee returned every time to the blue. During the following thirteen visits four slides were used (blue, red, yellow, white in two visits; blue, red, yellow, black in eleven visits), and the bee naturally showed greater hesitation and an increasing tendency to visit other colors than blue. Still it took up its load eight times on blue to once on white, once on red, once on yellow, and twice on black. In every instance where the bee selected another color than blue, it will be observed that it was after the slides had been transposed, or a color had been changed; and that with one exception it again returned to blue on the next visit. Of the total twenty-one visits fifteen were made to the blue, but not more than two to any other color. The bee steadily endeavored to remain constant to the blue, though this involved both loss of time and effort; and the number of exceptions is surprisingly few when we remember that before the close of the experiment the bee

had learned from experience that there was an ample supply of amber-colored honey on each of the four slides.

The purpose of my next experiment was to determine whether bees could readily determine a colored slide from a plain glass one. On September 10, 1908, I accustomed a line of Italian bees to visit a yellow slide. I then moved it six inches to one side, and exactly in its place I put a glass slide, under which there was no colored paper. A small quantity of honey was placed on the center of each slide. During twenty minutes the bees were carefully watched, and twelve visits to the yellow slide were recorded. A species of *Vespa* had built a nest not far away, and some of the workers also came to the yellow slide, and although they were an extraneous or foreign factor not directly connected with the experiment, their behavior was not without interest. Near the end of the time mentioned one of the wasps discovered the honey on the colorless slide and subsequently visited it. A bee attracted apparently by the presence of the wasp on this slide alighted beside it, but after a few moments flew across to the yellow.

I now transposed the slides, the distance apart remaining six inches as before. During ten minutes the Italian bees made eight and the wasps nine visits to the yellow slide. Only one visit was made to the colorless slide and that was by a wasp. Another wasp alighted on the colorless slide for a few moments before going to the yellow. There were a number of visits made by flies, all of which were to the yellow. In this experiment not only was the colored slide easily distinguished from the one without color, but it was apparently more attractive not alone to the bees, which had been trained to visit it, but to incidental visitors such as the wasps and flies. There were, moreover, no exceptions to the fidelity of the bees to the yellow color, as there were in the earlier experiments, when they were given the choice between two colors.

The preference of the bees for the yellow slide was, indeed, so marked that possibly it might be objected that

the plain glass slide was invisible, or at least very inconspicuous. Such a supposition would be a mistake, for while it was certainly less conspicuous than the yellow slip, it could yet be seen clearly by the aid of reflected light and the amber-colored honey at a distance of more than ten feet. A year later on October 11, 1909, this was established by experiment. Two black bees were trained to visit a plain glass slide. While they were absent, the slide was moved six inches to the right, and a blue slide, which owed its color to the floral leaves of the bee-larkspur (*Delphinium elatum*) was put in its place. One of the bees returned to the colorless slide. When it left I moved the colorless slide twelve inches to the right of the blue slide. In this position the bees visited it twice. I transposed the slides. Both bees returned to the colorless slide, and a little later one of them came again. As no visits had been made to the blue slide, there could be no question but that the bees saw the plain glass slide.

As the result of his experiments with artificial flowers Plateau assumes that the artificial colors of paper or of cloth appear to bees of a different tint or tone than do the colors of natural flowers, which to human eyes are apparently of the same hue.⁶ My own investigations lead me to believe that this assumption is not well founded, and is not required to explain the behavior of bees under the conditions described by Plateau. The discussion of this question, however, would lead to too long a digression from the subject under consideration, and must be deferred to some other opportunity. But in passing it may be remarked that the readiness with which Bethe and his followers assume new forces and powers to sustain theoretical positions is not a little amazing to the prosaic naturalist content to work with known factors.⁷

⁶ Plateau, F., "Les insectes et la couleur des fleurs," *L'Année Psychologique*, 13, 77. "Comment les fleurs attirent les insectes," 5th part, *Bull. Acad. roy. Bel.*, 3^{me} série, 34, 847-881, 1897. "Les fleurs artificielles et les insectes," *Mem. Acad. roy. Bel.*, 2^{me} série, 1, 3-103.

⁷ Bethe holds that the bees are led back to the hive by a wholly unknown force. "Dürfen wir Ameisen und Bienen psychische Qualitäten zuschreiben?" p. 77, Bonn, 1898.

There is the less need of delay for inquiring into this imaginary power of vision, since bees as easily distinguish between the colors of flowers as between those of colored papers.

As the result of more than twenty-six hundred experiments on the color sense of the honey-bee Hermann Müller was convinced not alone that they could distinguish colors, but that they exhibited color preference.⁸ Instead of colored paper he made use of floral leaves, which he placed between two object slides, the edges of which were afterwards sealed with a soluble gum. The slides employed by myself were made as follows: A grayish-white slip of cardboard three inches long by one wide was covered with the yellow rays of a garden sunflower, over which a glass slide of the same dimensions was placed and tied firmly with black silk thread. In like manner a blue slide was prepared from the blue perianth of the bee-larkspur (*Delphinium elatum*), and a red slide from three bright red flowers of the Zanzibar balsam (*Impatiens sultani*).

On September 29 I accustomed several yellow or Italian bees to visit the yellow or sunflower slide. The slide was then moved eight inches to the right, and in its place was put the blue slide made from the floral leaves of the bee-larkspur. There was a small quantity of honey as usual on the center of each slide. At the same time I removed three of the bees, leaving only one. The time was 3 o'clock P.M., and the slides were in the shade. The bee returned to the yellow.

The bee left for the hive, and I transposed the slides. It returned to the yellow.

The bee left for the hive, and I transposed the slides. It returned to the blue.

When the bee left for the hive, no change was made. It returned to the yellow.

As soon as the bee left for the hive I transposed the

⁸ Müller, H., "Versuche über die Farbenliebbareie der Honigbiene," *Kosmos*, 11, 273-99. Reprinted as a separate by R. Friedländer & Sohn, Berlin, 1883.

slides for the fifth time. Two bees returned, one of which alighted on the yellow, the other on the blue. There could be little doubt that the bee which alighted on the yellow was the one which was under observation. This decision was based partly on its appearance (young bees can easily be distinguished from old ones), and partly because it was probable that it would return to the yellow. Its subsequent behavior satisfied me that this conclusion was correct. The bee on the blue was removed.

The bee on the yellow left for the hive and I transposed the slides. It returned to the yellow.

The bee left for the hive and I transposed the slides. The bee returned to the yellow, but presently left it, described a few circles in the air, and then again settled on the yellow.

The bee left for the hive, and I transposed the slides for the eighth time. The bee returned to the blue, but soon left it, and after circling around in the air alighted on the yellow, where it remained.

The bee left for the hive and I transposed the slides. It returned to the yellow.

During ten visits in only one instance did it take up its load on the blue. The dominant power of the yellow color is well shown in the case where the bee alighted on the blue, on which there was an abundance of honey, but soon left it for the yellow. In many other experiments, in which the red slide was used as well as the yellow and blue, the bees as easily discriminated between natural colors as between those which were artificial.

On October 6 I performed the following experiment for the purpose of determining whether bees were more strongly influenced by a colored slide than by one without color. A red slide, prepared from the bright red flowers of *Impatiens sultani*, an exotic from Zanzibar, was placed on a white box in the sun and about a dozen bees were permitted to visit it for some time. Each of the blossoms was an inch in diameter. At 10 o'clock in the morning a plain glass slide was substituted for the red one, which

was moved six inches to the right. There was a liberal supply of honey on the center of both slides.

In a few minutes there were seven bees on the red slide and two on the colorless. The bees were now driven away, the slides transposed, and the distance apart increased to sixteen inches. Six bees and a fly (*Eristalis tenax*) soon came to the red slide, but only one bee came to the colorless. The number of bees on the red slide continued to increase until there were about eight,⁹ and it was difficult for some of them to reach the honey. In the meantime there were only two bees on the colorless slide.

The bees were again driven away and the slides transposed, the distance apart remaining sixteen inches. At the end of a few moments there were eight bees on the red glass, and one bee on the colorless. The slides were transposed, and once more eight bees and the syrphid fly came to the red, and only one bee to the colorless.

The bees were driven away, and the slides transposed. Very quickly five bees selected the red, and two bees and the syrphid fly the colorless. Later there were eleven bees on the red, and only two on the colorless. The bees on the red slide were so crowded that this may have had some influence in sending two of them to the colorless. The honey on the latter slide was amber-colored and could be seen at a distance of twelve feet, while at times its odor must have been stronger than that upon the red slide, since it was removed much more slowly.

It may be objected that the very marked preference shown by the bees for the red slide was the result of their having been accustomed to visit it first. If one bee had been employed, this might be admitted, but in the case of so many bees, it is improbable, since they would naturally avoid continually crowding and interfering with each other. If, however, the objection is well founded, then they should continue to give the preference to the red

⁹ As the bees were closely bunched together, and were frequently coming and going, it was impossible at this moment to count the exact number within one.

slide, when a bright-colored slide is substituted for the colorless one.

Accordingly a blue slide was substituted for the one without color, and at the same time the slides were transposed, the distance apart still remaining sixteen inches. The honey was disposed as a narrow band along the center of each slide in order that it might be more easily accessible to the bees. In ten minutes there were eight bees on the red and two on the blue. A little later there were ten bees on the red, and four bees and a wasp on the blue.

The bees were driven away and the slides transposed. In a few minutes there were three bees and a wasp on the red, and nine bees on the blue. Ten minutes later there were six bees and an *Erystalis tenax* on the red, and four bees on the blue. Two minutes later there were three bees and the syrphid fly on the red, and seven bees on the blue. Very quickly then after the blue slide was substituted for the colorless one, the bees ceased to exhibit a preference for the red slide, and sometimes visited the red and sometimes the blue in larger numbers. This experiment thus affords evidence not only that bees can distinguish colors, but that they are also influenced by conspicuousness.¹⁰

The experience of apiarists furnishes very conclusive evidence of the power of bees to distinguish colors. The hives are sometimes painted different colors in order that the bees may mark their location with greater certainty and avoid entering the wrong hive. A bee-keeper describes in *Gleanings in Bee Culture* how he painted his hives red, white and blue, in order that the bees might mark their location largely by color. I have, he states, adopted the red, white and blue plan, since 1880, and am so well pleased with the result that I am painting all my new hives this spring in the same colors. It enables the bees to avoid making mistakes and going into the wrong

¹⁰ Lovell, John H., "The Color Sense of the Honey-bee: Is Conspicuousness an Advantage to Flowers?" *AM. NAT.*, 43, 338-349, June, 1909.

hives. If you remove a white hive, many of the bees will pass the blue one on the one side and the red one on the other side, and go into the white hives further on. This shows conclusively that bees mark the position of the hive by color as well as by its environment.

I admit that where a few colonies are kept in one place there is very little danger of the bees mixing; but where you have long rows of hives in sheds, as we have in Salt River Valley, the three colors will avoid a great deal of confusion and save the lives of many bees and some young queens.¹¹

While this plan works admirably so long as the hives are not moved, it of course, gives very unsatisfactory results, if for any reason a hive is removed and one of another color is substituted for it. When a colony swarms naturally, says another apiarist, or is swarmed artificially, or for any reason the old hive body is removed, unless the new hive is of the same color as the old hive many of the bees will not return to it, but will scatter among the hives nearest to the old location, which are of the same color as the hive which has been removed. For example if the dwelling of the parent colony was white and if at the time of swarming an attempt was made to put the swarm in a blue hive a large part of the bees would refuse to enter it and would fly away to the nearest white hive, with the result that the new colony was materially weakened. He, therefore, found it more convenient to paint all his hives one color.¹²

Another bee-keeper placed his hives in two house-apiaries, each containing 150 colonies. The three end hives at each end of the shed or house were painted green. If now all the green hives at one end were removed, the bees instead of entering the hives nearest to the old location, which were painted a different color, flew to the

¹¹ Lessing, Wm., "Painting Hives," *Gleanings in Bee Culture*, 34, 1428, November 15, 1906. For this article I am indebted to Mr. H. H. Root, editor of *Gleanings in Bee Culture*.

¹² Kinyon, Irving, "Color of Hives; A Variety of Colors Undesirable," *Gleanings in Bee Culture*, 35, 262, February 15, 1907. Mr. Kinyon writes me that about one third to one half of a swarm would thus be lost.

green hives at the other end of the house apiary, and tried to enter them, even though they were closed.¹³

These statements are confirmed by the experience of W. Z. Hutchinson, an authoritative writer on American apiculture.

One spring I bought and brought home about forty colonies or hives painted a very dark gray, or almost lead color. They were set down in the apiary by themselves in four different rows. In the course of a few days I began transferring the bees from these hives into white hives, like the rest of the hives in my apiary. I took an end hive first. When the brood combs were set over into a white hive, and this hive set down where the old gray hive had been, the bees refused to enter it, but piled into the next hive in the row, which, of course, was gray like their old home. This hive was soon filled to overflowing, some of the bees hanging on the outside. I then transferred the combs from this hive to a white one, but the bees refused to enter it and piled into the next gray hive in the row. The hives were about three feet apart in the row. A bee is guided to its home by location as well as color, and after about four hives, or colonies, had been transferred, then some of the bees began to enter the new, white hives, as the gray hives were now so far from their old location that they perceived that they could not be their home. The same trouble was had in each row that was transferred.¹⁴

An excellent illustration of the effect of differently colored hives is given by Buttel-Reepen:

A weak afterswarm, mostly of young bees from a hive painted blue, dispersed among the masses of humming bees which were just taking their flight of orientation out of the other hives (which, as is usually the case in Germany, Switzerland and Austria, were standing close together), and settled here and there in little clumps. After a short time they flew back to the bee-house; but only a few found the right hive; the rest flew to other colonies, and to which? Only where a blue door invited them did they attempt an entrance but nowhere else. Unfortunately they were so hostilely received that the ground in front of all the hives marked blue was covered with dead bees.¹⁵

The experience of apiarists, therefore, both in America and Europe furnishes indubitable evidence that bees by thousands readily distinguish colors.

¹³ The experience of a neighbor of Mr. Kinyon and described by him in a letter to the writer.

¹⁴ W. Z. Hutchinson, editor of *Bee Keeper's Review* and author of "Advanced Bee Culture" in a letter to the writer.

¹⁵ Buttel-Reepen, "Are Bees Reflex Machines?" p. 38, translated by Mary H. Geisler.

Additional observations might easily be given, but those presented appear sufficiently conclusive. It has been shown that bees can distinguish between the colors of papers, of flowers, and of painted hives, and that they are more strongly influenced by a colored slide than by a plain glass one. It may well be doubted whether they would ever have been capable of making long journeys afield for nectar and pollen, if this visual power had been wanting. To those unfamiliar with the habits of bees, it will occasion surprise that the bee after it had discovered and began sucking honey on the red slide (to take for illustration the ninth visit of the first experiment) should have voluntarily left it and gone back to the blue for the larger part of its load. But its behavior in this instance is quite in accord with the principles of bee psychology. Bees, as Forel states as the result of his own and the experience of Huber, Buttel-Reepen and Wasmann, very rapidly form habits, and their attention becoming fixed by frequent repetitions is not easily diverted.¹⁶ When the bee, which had been trained to visit the blue slide, alighted on the red, it was disturbed by the difference of hue and suffered a certain degree of mental disquietude, which was not allayed until it returned to the blue.

All of the higher Hymenoptera probably possess the power of distinguishing colors. This has been established for the social wasps of the genus *Vespa* by the interesting experiments of the Peckhams. One of their experiments very strikingly shows the value of color contrasts, and effectively refutes Plateau's assertion that all flowers might be as green as their leaves without their pollination being compromised.

We once placed some dark red nasturtiums on light yellow paper near the nest, and found that more than one third of the homecoming wasps flew to them and hovered over them before entering. When light yellow nasturtiums, nearly matching the paper in color, were substituted only one out of thirty-six noticed them; and as the odor was as strong in

¹⁶ Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 20.

one case as the other, it would seem that the color was the attracting force.¹⁷

It remains to consider the numerous instances where bees visit indiscriminately the differently colored varieties of the same species of flower. *Zinnia elegans* displays white, yellow, orange, red and purple varieties; *Dahlia variabilis* white, yellow, orange, red and purple; and *Centaurea Cyanus* red, white, blue and purple flowers. When visiting any one of these species for nectar bees pass freely from flowers of one color to those of another. Plateau says:

If in the case of the same plant species the varieties of distinct color are in equal quantities, the insects pass without order from one color to another.¹⁸

One summer in my garden a single plant of the scarlet runner (*Phaseolus multiflorus*) produced pure white blossoms, which offered a striking contrast to the normal bright scarlet racemes; but honey-bees and bumblebees (*Bombus terricola*) visited both as though they had been of the same hue. Bees likewise ignore the differences of color in the white, rose-red, and purple flowers of *Scabiosa atropurpurea*. But this behavior on the part of bees furnishes no evidence whatever that they can not distinguish colors.

Honey-bees in collecting pollen and nectar are faithful as a rule to a single species of flower—they exhibit “flower fidelity.” This is evidently for their advantage, since if they were to pass continually from flowers of one form to those of another much time would be lost in locating the nectar. Even whole colonies may follow this order. Mr. M. H. Mendleson, of Ventura, California, one of the largest honey-producers on the Pacific coast, relates that

In 1884, one colony out of 200 gathered exclusively from an abundance of mustard bloom; the 199 gathered from the sages.¹⁹

¹⁷ Peckham, George W., and Elizabeth, “Wasps Social and Solitary,” p. 6, 1905.

¹⁸ Plateau, F., “Les Insectes et la couleur des fleurs,” *L'Année psychologique*, 13, 78.

¹⁹ Mendleson, M. H., *Gleanings in Bee Culture*, October 1, 1908, 36, 1204.

But if the species are closely allied in form and color, as among the buttercups, spiræas and golden-rods, the bees do not carefully discriminate between them. Yet even in these genera the honey-bee often exhibits a remarkable power of distinguishing between allied species, even when they are of the same color. I have described in the AMERICAN NATURALIST how in an upland pasture honey-bees showed a marked preference for the flat-topped corymbs of *Solidago lanceolata* (*Euthamia graminifolia*) to the paniced inflorescence of *S. rugosa*.

They were repeatedly seen to leave *S. lanceolata*, and after flying about but not resting on the flowers of *S. rugosa* return to the plants they had left only a few moments before. In another instance a bee was seen to wind its way among the plants of the latter species until it found an isolated plant of *S. lanceolata*. A plant of each of the above species was bent over so that the blossoms were intermingled, appearing as a single cluster; a honey-bee rested on *S. lanceolata* and it seemed very probable that it would pass over to the flowers of *S. rugosa*, but such was not the case, for presently it flew away to another plant of the former.²⁰

The bees must, therefore, have perceived differences between these two species of *Solidago*, though they occasionally ignored them.

When a plant species displays variously colored flowers, it is obvious that they are alike in shape, odor and nectar, and differ in color alone. Under these circumstances it is for the advantage of bees to pass from one color to another, and this they speedily learn to do. In an earlier paper I have pointed out that form is a more important factor than color in determining the visits of the long-tongued bees and butterflies.²¹ This conclusion is confirmed by Dr. Graenicher in a very important contribution on the pollination of the Compositæ. After a careful comparison of the effect of tube length, color, and odor on the limitation of visitors, he says:

It may be stated that according to the results obtained from a study

²⁰ Lovell, John H., "The Colors of Northern Gamopetalous Flowers," AM. NAT., 37, 453, July, 1903.

²¹ Lovell, John H., "The Colors of Northern Gamopetalous Flowers," AM. NAT., 37, 452 and 477-8, July, 1903.

of our Compositæ the proportion of short-tongued to long-tongued visitors in these flowers is determined by tube length more than by any other character of the flower.²²

In the flowers under consideration the important barrier of difference in form is absent.

In the following experiment it is shown how a bee soon learns to visit colors indiscriminately. On September 22 after a black bee had been accustomed to visit a slip of blue paper, a series of seven differently colored slides were arranged in the following order: black, green, blue, purple, red, white, yellow, orange. The slides were three inches apart, or twenty-two inches from end to end; and there was a small quantity of honey on the center of each. The bee returned the first time to the blue, the second time to the purple, the third time to the purple, the fourth time to the blue, the fifth time to the purple. It will be observed that the bee ceased at once to discriminate between the blue and the purple—the two slides being adjacent and allied in color. On its fifth visit before alighting the bee hovered over the different colors for many seconds, and later left the purple for the red, whence after a brief stop it flew away to the hive.

During the next three visits the bee devoted much time to the examination of the slides, but subsequently it paid little attention to the colors. When the bee returned from the hive, it flew about for a long time, touched on the orange, but immediately left it and went to the blue. On its seventh visit the bee after describing a few circles in the air, touched on the red, then on the blue, went back to the red, and finally stopped on the blue. The colors were arranged in the following order: black, red, blue, white, green, orange, purple, yellow. On its eighth journey before alighting the bee flew from the vicinity of the blue over to the yellow and back to the blue where it remained. There could be no doubt that it was examining the slides, as it flew close to them touching them at times.

I transposed the blue and green slides so that the order

²² Graenicher, S., "Wisconsin Flowers and their Pollination—Compositæ," *Bull. Wis. Nat. Hist. Soc.*, 7, 42, April, 1909.

was black, green, white, blue, orange, purple, yellow. On its ninth visit the bee returned to the red; on the tenth to the green, then going to red and white, but finally coming back to the green. On its eleventh and twelfth visits the bee returned to the blue. I transposed the blue with the yellow and the red with the purple so that the order of the colors was black, purple, green, white, yellow, orange, red, blue. The thirteenth and fourteenth visits were made to the yellow, the fifteenth to the white, the sixteenth and seventeenth to the yellow, the eighteenth and nineteenth to the blue—on the last visit it was disturbed by a wasp and went to the orange. The twentieth visit was to the yellow, the twenty-first to the green, and the twenty-second to the yellow.

It is evident that at the beginning of this experiment the behavior of the bee was widely different from what it was at its close. Habituated to visit the blue slide, it continued constant to this slide or the allied purple during its earlier visits; though again and again by means of its visual and olfactory senses it examined and compared the other slides, as has been described. Repeated transpositions of the blue paper gradually weakened its fidelity to this color, until at last similarity of form, honey and odor prevailed over dissimilarity of color, and the bee visited the slides indiscriminately. This result might also have been brought about by permitting the bee to remove all the honey from the blue slide, when it would have turned from necessity to one of the other colors. This is no doubt what happens in nature. A bee finds usually in one flower only a portion of its load of nectar, and so is compelled to examine other blossoms, which, if they are alike in form, it will soon visit without order even though they differ in color. If there are a number of bees, their efforts to avoid visiting the same slide or flower will greatly hasten the breaking down of the color barrier. In a location frequented by a few bees for honey I put out the following series of colors: white, blue, green, black, red orange, purple. In a few minutes there was a

bee on every color save black and orange, and a little later there was a bee on each of these slides. The total number of bees was twelve.

That bees can by the aid of their sense perceptions draw "simple instinctive inferences" has also been shown experimentally by Forel. In a bed of dahlias of various colors he mounted red, white and blue paper flowers, in each of which was placed a drop of honey. A red, a white flower and a rose-colored piece of paper with a dry dahlia disc were each brought to the attention of a bee. Thenceforth these three bees, which were marked on the back with blue, yellow and white paints, returned regularly to the artefacts and no longer visited the dahlias.

The painted bees entirely of their own accord, undoubtedly through an instinctive inference from analogy, discovered the other artefacts as soon as their attention had been attracted by the honey on one of them, notwithstanding the artefacts were some distance from one another and of different colors. For were not the dahlias, too, which they had previously visited of different colors? . . . It would be a fallacy to conclude from this that they do not distinguish colors.²³

CONCLUSIONS

Bees easily distinguish colors, whether they are artificial (paints, dyes, etc.) or natural ("chlorophyll") colors.

Bees are more strongly influenced by a colored slide than by one without color.

Bees, which have been accustomed to visit a certain color, tend to return to it habitually—they exhibit color fidelity.

But this habit does not become obsessional, since they quickly learn not to discriminate between colors when this is for their advantage.

²³ Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 27.